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AUSTRALIAN CARABID BEETLES V.[1] TRANSITION OF WET FOREST FAUNAS FROM NEW GUINEA TO TASMANIA

By P. J. Darlington, Jr.
Museum of Comparative Zoology, Cambridge, Mass.

Introduction

Beetles of the family Carabidae (predaceous ground beetles) are numerous in tropical rain forest in New Guinea and numerous also (but less diverse) in cool south temperate rain forest in Tasmania, but no species and hardly any genus is common to the two faunas, and even the dominant tribes are different. However there is no single boundary between the New Guinean and Tasmanian faunas, but a broad and complex transition, which I shall try to describe.

My interest in this part of the world began with the Harvard Australian Expedition of 1931-1932, when I collected Carabidae in eastern Australia north to part of the Cape York Peninsula, as well as in southwestern Australia. In 1943-1944 I spent eleven months in New Guinea as an army entomologist, and was able to collect Carabidae especially in lowland rain forest at Dobodura, Papua, while hospitalized there, and in mountain forest on the Bismarck Range, Northeast New Guinea, in lieu of leave. I have sorted and arranged my own and much borrowed material and am now more than half way through writing "The Carabid Beetles of New Guinea" (see Darlington 1952), so that I have a good knowledge of New Guinean Carabidae. Recently, from December 1956 to June 1958, I have been again in eastern Australia, traveling and living in a small truck with my wife and fourteen-year-old son, and collecting Carabidae in practically every important piece of wet forest from the northern tip of Cape

[1]Earlier parts of this series are listed in the reference list at the end of this paper.

York to the southern tip of Tasmania.[2] A brief itinerary with maps and list of localities has been published (1961). Information and collections obtained during this trip have enabled me to correlate other information and write the present paper. New genera and species referred to now (but not by name) will be described in forthcoming numbers of *Psyche* and *Breviora*.

The Forests

My "wet forests" are rain forests as classified in "The Australian Environment" (CSIRO 1950, 77-96). That is, they are dense, evergreen (non-deciduous) forests with closed canopies, often (in tropical rain forest) with many woody vines, but with comparatively little low vegetation, the ground being covered with dead leaves and leaf mold rather than grass or herbs.

Two main types of rain forest exist in the Australian Region: tropical (including subtropical) (Figs. 1, 2) and south temperate (Figs. 3, 4). Tropical rain forest is widely distributed in New Guinea at low and middle altitudes, although in the drier country of southern New Guinea it is replaced by op n savannah woodland like that of much of northern Australia. Tropical rain forest occurs also on the eastern edge of Australia in separate tracts spaced irregularly from parts of Cape York south through Queensland and northern New South Wales (map, Fig. 6). The best of this forest in tropical and subtropical Australia as well as in New Guinea is real, Malaysian-type rain forest, although some tracts in Australia are lighter and seasonally drier, and light rain forest sometimes grades into semi-deciduous monsoon forest.

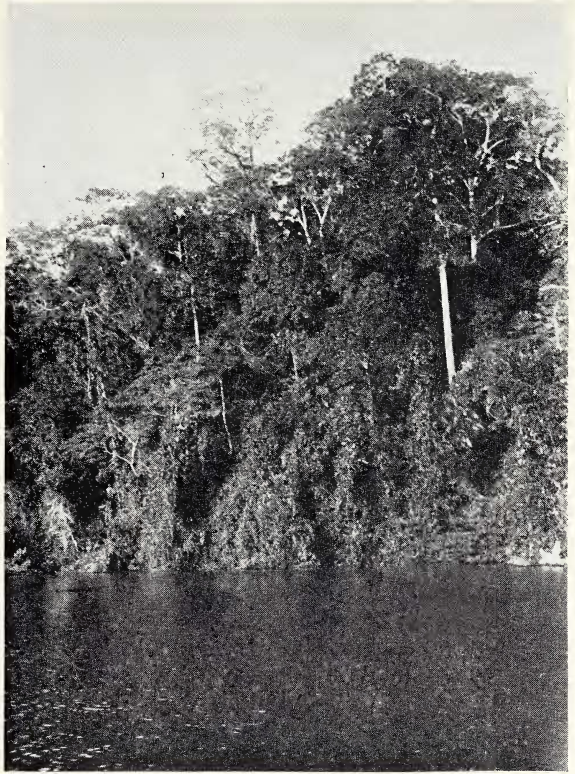
The northernmost rain forest in Australia is the tip-of-peninsular (Lockerbie or Somerset) tract on the tip of Cape York. It is lowland rain forest, but somewhat depauperate (see p. 17).

[2]This trip was supported in part by a fellowship of the John Simon Guggenheim Memorial Foundation. I am especially indebted to Dr. L. J. Webb, of the Commonwealth Scientific and Industrial Research Organization, for information on the distribution of rain forest in Queensland, to many members of the Queensland Department of Forestry who aided or guided us in the field, and to Mr. P. J. Killoran, of the Queensland Department of Native Affairs, who arranged our visit to Bamaga and the tip of Cape York. I very much regret that I do not have space to acknowledge other assistance in detail here.

Explanation of Plate 1

Fig. 1. Tropical rain forest, Lake Barrine, Atherton Tableland, North Queensland (P. J. D. 1932).

Fig. 2. Interior of tip-of-peninsular (tropical) rain forest, from edge of new clearing, Lockerbie, Cape York, Queensland (P. J. D. 1958). This is the habitat of *Mecynognathus*.



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2

3

4

Next in order southward is a gap more than 100 miles wide of drier, open savannah woodland (Fig. 5) in which may be an isolated piece of rain forest near the head of the Jardine River, unknown biologically (Brass 1953, pp. 154, 161).

Next is the mid-peninsular rain forest system. It extends irregularly and with perhaps slight interruptions from near Iron Range and Mt. Tozer south to the "Rocky Scrub" east of Coen. Altitudinally it extends from near sea level (*e.g.* at Iron Range) to about 2,000 ft. on the higher summits of the McIlwraith Range. It includes fairly heavy rain forest, although its quality varies locally.

Fig. 5. Rather dry savannah woodland northeast of Coen, Cape York peninsula. (P. J. D. 1932). Such woodland is an effective barrier to rain forest Carabidae in the tropics.

Next, after another gap more than 150 miles wide of drier, open woodland, is the base-of-peninsular or main tropical rain forest system of North Queensland. Outlying pieces of semi-rain forest of this system are within sight of Cooktown, and heavier rain forest begins on the coastal mountains (Mt. Amos, Mt. Finnigan) about 20 miles to

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Explanation of Plate 2

Fig. 3. South temperate rain forest, Lake St. Clair, Tasmania (P. J. D. 1957). On left is transitional wet forest with overstory of big eucalypts; center, heavy rain forest including *Nothofagus*.

Fig. 4. Interior of old south temperate rain forest, Cradle Valley, northern Tasmania (courtesy Mr. H. J. King, Honorary Photographer, and Mr. Frank Ellis, Director, Queen Victoria Museum, Launceston).

the south. From here an irregular system of good rain forests extends somewhat discontinuously but with no very wide breaks south to and across the Atherton Tableland and farther south along a series of plateaus and ranges to the Mt. Spec plateau (Paluma Range) almost within sight of Townsville. Much of this forest system lies between 1,000 and 5,000 ft. altitude, but areas of good rain forest belonging to it occur (or occurred before being cleared) also on the coastal plain east of the Atherton Tableland and in the Mossman-Daintree region.

From the southern end of the main tropical rain forest system to below Rockhampton is a gap of nearly 500 miles of dry, open woodland broken only (so far as I know) by two noteworthy islands of rain forest. One is at about 3,000-4,000 ft. on the crest of the Elliot Range, within sight of (southeast of) Townsville but separated from the northern rain forests by a low, comparatively dry valley. The other, more important island of rain forest is on the Eungella Range about 40 miles inland from Mackay, at about 2,000-4,000 ft. altitude. Scattered fragments of semi-rain forest, for example near Proserpine (Repulse Bay) and Yepoon (Byfield), are relatively unimportant so far as carabid distribution is concerned.

South of Rockhampton, in the edge of the south temperate zone, begins what I call the subtropical rain forest system. The first piece of (rather poor) rain forest of this system is on Mt. Jacob east of Many Peaks. Other tracts are widely scattered in southeastern Queensland at low altitudes as well as on mountains (Blackall Range, Bunya Mts., Mt. Tamborine, McPherson Range on the New South Wales border, etc.). The different forest tracts vary in quality, but the best of them approximate tropical rain forest. This system of rain forests extends into northeastern New South Wales at rather low altitudes, although much of it has now been cleared. The more important pieces that still remain are listed and briefly described in my published locality list (1961). The most southern *good* tract that seemed to me to be tropical-type rain forest is on "Mt. Dorrigo", on the lower (eastern) edge of the Dorrigo Plateau, at about 30° 20′ S., but small pockets of more or less similar forest occur still farther south, even south of Sydney, especially in wet ravines.

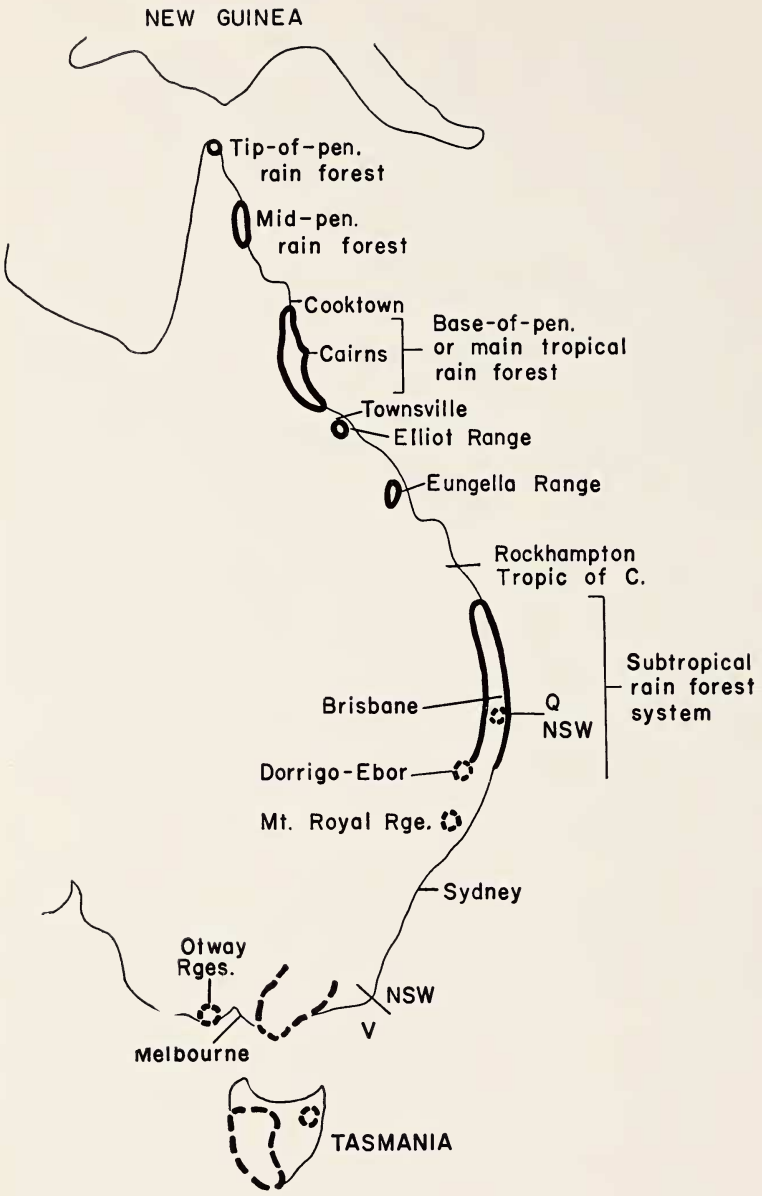
South temperate rain forest (see again Figs. 3, 4) is different in aspect from tropical rain forest (fewer vines, etc.) and different botanically, often dominated by southern beeches (*Nothofagus*). Such forest is widespread in southwestern Tasmania and occurs in isolated tracts elsewhere in Tasmania (see paper referred to above for details). Isolated tracts of similar forest occur on plateaus and mountains in southern Victoria including the Otway Ranges southwest of

Melbourne and some of the southern "Victorian Alps" east of Melbourne. This kind of forest occurs also, at wide intervals, on isolated plateaus in eastern New South Wales, notably on the plateau of the Mt. Royal Range (Barrington Tops and Tomalla Tops) at about 31° 50′ S. and on the higher part of the Dorrigo-Ebor Plateau (especially at Point Lookout in New England National Park) at about 30° S. Both these plateaus reach about 5000 ft. above sea level. The northernmost *Nothofagus* in Australia is still farther north, on the southern border of Queensland, where small tracts of old trees exist on the highest points of the McPherson Range, at about 28° 20′ S. and 4,000 ft. altitude. *Nothofagus* does not occur on the mountains of tropical North Queensland but is dominant in New Guinea in mountain forests between about 6,500 and 10,000 ft. (Womersley and McAdam 1957, p. 25). However, south temperate groups of Carabidae do *not* occur in the New Guinean *Nothofagus* forests.

The distribution of tropical (including subtropical) and south temperate rain forest is shown, rather diagramatically, on the accompanying map (Fig. 6). The map is based partly on the vegetation map in "The Australian Environment" (CSIRO 1950, pp. 88-89) and on Brass's (1953, p. 152) map of Cape York rain forests, but many details are modified according to my own observations. In most cases rain forest is not continuous within the boundaries shown, but occurs as irregular, sometimes discontinuous tracts and strips interspersed with savannah woodland (in the north) and/or sclerophyll forest (in the south). The two kinds of rain forest overlap widely in New South Wales. Within the area of overlap south temperate rain forest is usually above (at higher altitude than) tropical rain forest, but there is some mixing.

The Carabidae

The wet-forest Carabidae of New Guinea and Australia, including Tasmania, are numerous, diverse, and complex in ecology and distribution. They form three general ecological groups. Those that live on the ground without being specially associated with surface water are mesophiles or *geophiles*. Those that live on the ground beside streams or ponds or in swamps are *hydrophiles*. And those that live on tree trunks or in foliage above the ground are *arboreal*. According to my (1943, p. 41) rough analysis of the Australian carabid fauna, at least half the species are geophiles, not quite a quarter hydrophiles, and not quite a quarter arboreal. The carabid fauna of New Guinea divides in something like the same way, although I cannot yet give exact figures.


NEW GUINEA
Tip-of-pen. rain forest
Mid-pen. rain forest
Cooktown
Cairns
Base-of-pen. or main tropical rain forest
Townsville
Elliot Range
Eungella Range
Rockhampton Tropic of C.
Subtropical rain forest system
Brisbane
Q
NSW
Dorrigo-Ebor
Mt. Royal Rge.
Sydney
Otway Rges.
NSW
V
Melbourne
TASMANIA

State of wings of Carabidae is correlated with ecology and distribution. Most Carabidae in most parts of the world have fully developed inner wings and can fly, but some have lost their wings (except for vestiges) and become flightless. The Australian carabid fauna includes an unusually large proportion of flightless species: according to my rough analysis (*loc. cit.*), nearly 45% of all Australian Carabidae have atrophied wings, and many genera and even some tribes are wholly flightless. Most hydrophiles and arboreal forms have retained their wings and can fly, but about 75% of Australian geophile Carabidae are flightless, and flightless groups are common everywhere in Australia, at low and high altitudes and in wet and dry climates, and some are well represented in the tropical as well as the temperate parts of the continent. In New Guinea flightnessess is rare among lowland Carabidae. This accords with the general rule that most Carabidae in most wholly tropical lowland areas are winged. On mountains in New Guinea, however, as on many tropical mountains elsewhere, flightless geophile Carabidae are numerous.

New Guinea-Tropical Australian Relationships

Probably the first fact that strikes entomologists collecting in the rain forests of tropical Australia is that some of the insects are species that occur in New Guinea. This is expected. The Australian rain forests themselves are predominantly New Guinean (or Malaysian) both in aspect and in botanical relationships (CSIRO 1950, pp. 95-96; Brass 1953, p. 154); many mammals in the North Queensland rain forests belong to New Guinean genera or even species; and so do many birds. Some Carabidae are common to New Guinean and Australian rain forests. For example *Syleter papua* Darl. extends to the tip of Cape York, living on the ground in shaded swamps. *Morion longipenne* Putz. of New Guinea extends to the main North Queensland rain forests, on and in fallen logs. And *Violagonum violaceum* (Chd.) is common in rain forest in New Guinea and eastern Australia south at least to near Rockhampton, in accumulations of dead leaves on the ground and in thick foliage. Besides shared species like these (there are many others among Carabidae) the New Guinean and Australian rain forests share some geographically restricted genera, for example *Platycoelus (Chlaenioidius)*, *Loxandrus*, and *Stricklandia*,

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Explanation of Plate 3

Fig. 6. Distribution of rain forests in eastern Australia. Solid lines enclose principal areas of tropical (including subtropical) rain forest; broken lines, of south temperate rain forest. In most cases rain forest is not continuous within the boundaries shown but occurs in discontinuous or scattered tracts. See text for further details.

as well as many more-widely distributed genera. Up to a point, therefore, the Carabidae agree with the forest trees, mammals, and birds in showing a considerable number of species and genera common to the rain forests of New Guinea and tropical Australia.

When I was collecting on the Atherton Tableland in northeastern Australia in 1932, I found not only many Carabidae of obviously New Guinean groups but also, in rain forest, many species of Australian groups not known to occur in New Guinea. Included were striking endemic species of *Notonomus, Trichosternus, Leiradira, Pamborus,* and *Mystropomus.* Knowing, as I did, that the rain forests of Australia and New Guinea had much in common, and knowing that the Carabidae of New Guinea were poorly collected, I imagined in New Guinea a rich fauna of the genera just named, perhaps in rain forest at middle altitudes, but wholly unknown. It was a sort of El Dorado for the future, to a young and enthusiastic carabid student. But now that I have collected in New Guinea and seen thousands of Carabidae collected there by other persons, I know that this El Dorado does not exist, and I know why. All the Carabidae common to the New Guinean and Australian rain forests are winged and probably fly. All the genera mentioned above as represented in rain forest on the Atherton Tableland are wholly flightless, and I know now that there is no direct relationship between any flightless Carabidae of the New Guinean and Australian rain forests.[3]

The difference between the flightless Carabidae of Australia and New Guinea goes far beyond mere differences of species and genera. The composition and origins of the two faunas are fundamentally different. Flightless Carabidae are numerous everywhere in Australia, even at low altitudes in the tropical part of the continent including Cape York. Many of the species belong to wholly flightless genera or even flightless tribes that have evidently been in Australia a long time. Derivatives of old Australian flightless groups dominate the flightless ground-living carabid fauna of tropical rain forest in Australia. In New Guinea, in contrast, no primarily flightless groups of Carabidae occur at low altitudes. A very few species of the primarily winged

[3]If tiger beetles are considered Carabidae, *Tricondyla aptera* Ol. is an exception to this rule. The genus *Tricondyla* is primarily Oriental and is wholly flightless. Nevertheless *T. aptera* has reached New Guinea, probably rather recently (it is only slightly differentiated there), and has got beyond New Guinea to the mid-peninsular rain forests of Cape York. (It has reached the Solomon Islands and New Hebrides too.) It is a good sized (nearly an inch long), big-eyed, ant-like, active insect, which lives on tree trunks in rain forest. It has probably dispersed on floating trees, which ground-living Carabidae are not likely to do.

genera *Clivina, Tachys, Lesticus, Platycoelus,* and *Loxandrus* have undergone wing atrophy at low altitudes in New Guinea (Darlington in press), but they have evidently done it recently, *in situ.* Some of the species are still dimorphic, with fully winged individuals occurring with the short winged ones, and all the short winged lowland species are closely related to long winged ones that still exist in New Guinea. It is only above about 5000 ft. in the mountains that flightless Carabidae become numerous in New Guinea, and they too have apparently undergone wing atrophy *in situ.* That is, they have been derived on the mountains of New Guinea from winged ancestors, and do not represent flightless stocks of other regions. This is my conclusion after making formal studies of the New Guinean representatives of the two principal tribes concerned, the Agonini (Darlington 1952, especially table p. 108) and Pterostichini (in press).

Besides the change of specific flightless stocks from New Guinea to Australia there is a change of dominance of tribes. In New Guinea, Agonini are much more numerous than Pterostichini, and most flightless Carabidae of the island are agonines. But in Australia, even in the tropical rain forest, Pterostichini are overwhelmingly dominant and include most of the flightless forms. This striking shift of dominance is further discussed on page 22.

The first important finding of the present study, then, is that, although the rain forests of New Guinea and tropical Australia are similar and share many species of plants, mammals, birds, and winged insects including many winged Carabidae, they have wholly different faunas of flightless Carabidae, which differ not only in taxonomic details but also in general ecology (in relation to altitude), in origin of the flightless stocks, and in relative dominance of tribes.

Transition in Australia: South from the Tropics

Now to be considered is the transition of wet forest carabid faunas within the limits of Australia and Tasmania.

Five important genera of flightless geophile Carabidae are mentioned above as occurring in rain forest on the Atherton Tableland. Of these five genera, *Notonomus* is most dominant. It is a genus of about 100 species, confined to eastern and southeastern Australia and Tasmania except for one species isolated in southwestern Australia. The genus' northern limit is between Daintree and Cooktown. It is represented by several species (some very localized) in the main tropical rain forest system of North Queensland, where it seems to be confined to rain forest. It is well represented in the subtropical rain forests of South Queensland and northern New South Wales and south through

eastern New South Wales and southern Victoria; in these areas some species occur not only in rain forest (including south temperate rain forest) but also in wet sclerophyll forest and good savannah woodland. However only two groups of the genus reach Tasmania and only one group (two related, primarily allopatric species) occurs in rain forest there.

Trichosternus is a genus of 25 or more species confined to eastern Australia, except that one species is isolated in southwestern Australia (Darlington 1953, p. 94). The genus' northern limit is between Daintree and Cooktown. It occurs (several species, some very localized) throughout the main rain forest system of North Queensland, where it is apparently confined to rain forest. It is well represented also in the subtropical rain forest system of South Queensland and northern New South Wales, and in this area some species occur in savannah woodland as well as in tropical-type rain forest, and some have entered south temperate rain forest on the Dorrigo-Ebor plateau and the Mt. Royal Range. The southern limit of the genus is somewhere in east-central New South Wales, probably not far north of Sydney.

The northern limit of *Leiradira* (or of the group of genera that includes *Leiradira*) is between Daintree and Cooktown. This genus too occurs in much of the main tropical rain forest system of North Queensland, being represented there by several distinct species each more or less localized, but the genus may be absent in the southern extension of the main tropical rain forest system south of the Atherton Tableland. It is represented also by several species in the subtropical rain forests of South Queensland etc. Its southern limit is apparently on the lower, eastern edge of the Dorrigo plateau. It is confined to eastern Australia. It is wholly or chiefly a rain forest genus in all parts of its range.

The three preceding genera are all Pterostichini. All their species are flightless geophiles. Additional flightless geophile pterostichines are localized in all the different rain forest areas of Australia from Cape York to Tasmania. Examples are *Mecynognathus* in the tip-of-peninsular forests; *Paranurus* in the mid-peninsular forests; *Loxogenius* and undescribed genera in the main tropical rain forest system; *Nursus s. s., Liopasa, Ceratoferonia, Zeodera,* and *Notolestes* in the subtropical rain forest system; *Loxodactylus* in the wet forests of southern Victoria; and *Rhabdotus* in those of Tasmania. (It should be added that Australia possesses many winged pterostichines as well as these and other flightless genera.)

Of non-pterostichines, *Pamborus* is noteworthy. It is confined to eastern Australia and is one of the two known genera of the tribe Pamborini. (The other is monotypic *Maoripamborus* in New Zealand — Brookes 1944.) The northern limit of *Pamborus* is probably near Cooktown. Four species of the genus occur in the main tropical rain forest system of North Queensland, chiefly or wholly in rain forest. Six other species occur in South Queensland and New South Wales. Some of them occur mainly in (sub)tropical rain forest, but *viridis* inhabits savannah woodland and some other species occur in open woods as well as rain forest, and some enter south temperate rain forest on the high plateaus of north-central New South Wales. The southern limit of the genus is near the Shoalhaven River about 70 miles south of Sydney. (Old records for Victoria are probably errors.)

The genus *Mystropomus* is the only Australian representative of the pantropical tribe Ozaenini. The genus is confined to eastern Australia. Its northern limit is between Daintree and Cooktown. A single species (two subspecies) occurs throughout the main tropical rain forest system of North Queensland, and is apparently confined to rain forest. Another, variable species (two subspecies) occurs in the subtropical rain forest system, and extends into more open woodland. The southern limit of the genus is apparently near Sydney.

These five genera dominate the flightless geophile carabid faunas of the main tropical and subtropical rain forest systems of eastern Australia. Their distribution is notable in several ways. All five genera reach an approximately common northern limit, north of Daintree and south of or near Cooktown. All five genera are widely distributed both in the main tropical and in the subtropical rain forest systems. These two forest systems are separated by a wide barrier of comparatively dry, open forest in which is one important "island" of rain forest, on the Eungella Range west of Mackay, and all five of the genera in question are represented there.[4] In the tropics, these genera occur only or chiefly in rain forest,[5] although most of them enter opener forest too in the south temperate zone.

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[4]Of the 5 genera in question on the Eungella Range, the one *Pamborus* has close relatives in both North and South Queensland. The one *Mystropomus* is a South Queensland species. Of 2 *Trichosternus*, one probably belongs to a South Queensland group and the other is doubtful. The one *Notonomus* belongs to a North Queensland group. And the one *Leiradira* belongs to a South Queensland subgenus. These genera in the Eungella rain forest therefore show 2 close ties with North Queensland (in *Pamborus* and *Notonomus*) and 4 with South Queensland.

[5]*Trichosternus cordatus* Chd. occurs outside rain forest in the southern edge of the tropics.

Southward, through New South Wales, rain forest of (sub)tropical type diminishes in area and quality, and the Carabidae associated with it diminish too. Of the five genera just discussed, *Leiradira* may not extend south of the Dorrigo. *Trichosternus, Mystropomus,* and *Pamborus* go a little farther south, reaching different limits probably in this order, but do not reach Victoria. And *Notonomus* reaches Victoria (in numbers) and Tasmania (only one stock in rain forest). Toward their southern limits, all these genera, except *Leiradira,* occur not only in tropical-type rain forest but also in opener forest, and all, except again *Leiradira,* have entered or even evolved endemic species in south temperate rain forest on the Dorrigo-Ebor plateau and the Mt. Royal Range.

Transition in Australia: North from Tasmania

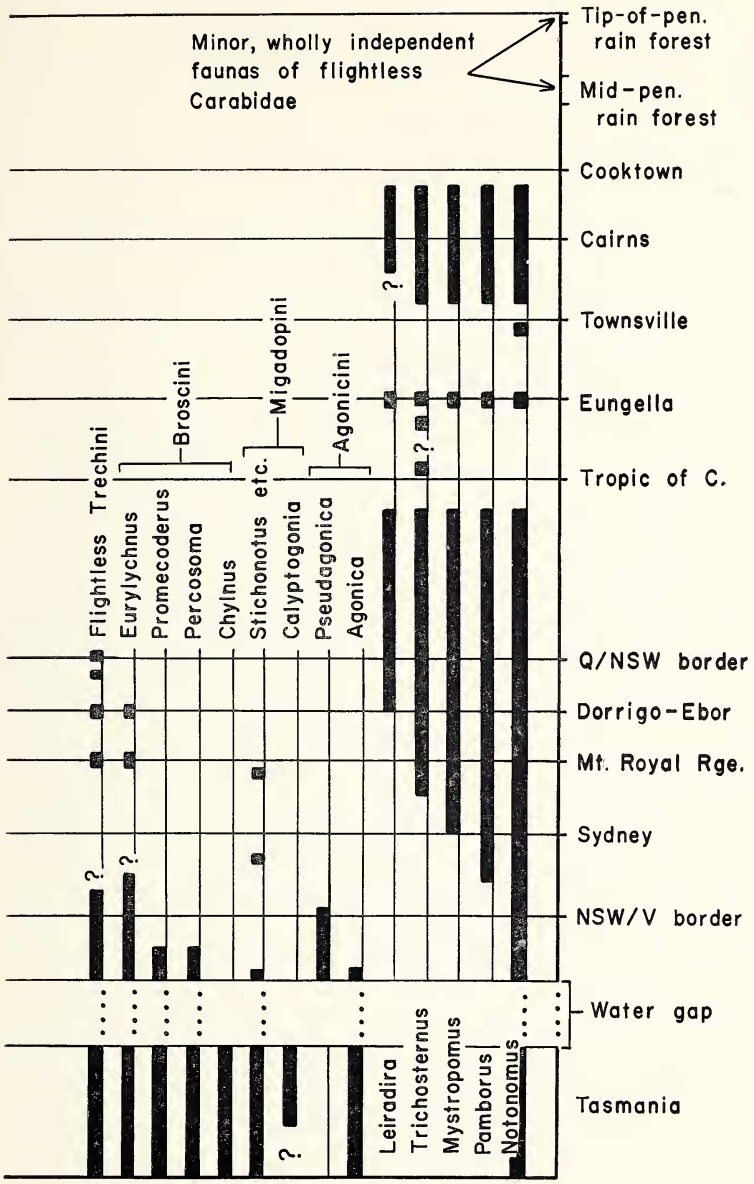
The ground-living Carabidae of the south temperate rain forest of Tasmania are dominated by or include flightless genera of four special tribes in addition to the more widely distributed Pterostichini, Licinini, etc.

The tribe Broscini is well represented in both the north and the south temperate zones of the world (Ball 1956) but is absent in the tropics or nearly so. Some northern broscines have well developed wings, but I think that all those of the southern hemisphere have atrophied wings and are flightless. Four genera occur in Tasmania. *Promecoderus* is represented there by several rain forest species and by other species that live in drier, opener woodland. The genus is widely distributed across southern Australia, but chiefly in dry forest and arid country, although one or two species occur in rain forest in Victoria. Of the other Tasmanian genera, *Chylnus* is confined to Tasmania, in wet forest. *Percosoma* occurs in Tasmania and the mountains of southeastern Victoria, in wet forest. And *Eurylychnus* occurs in Tasmania, southern Victoria etc. including the Otway Ranges, and east and north into southern New South Wales, and two separate stocks of the genus have species isolated (chiefly in south temperate rain forest) on the Mt. Royal Range and the Dorrigo-Ebor plateau. The latter is the northern limit of wet-forest broscines in Australia.

The tribe Trechini (subfamily Trechinae of Jeannel 1926-1928)

Explanation of Plate 4

Fig. 7. Diagram of transition of selected flightless geophile Carabidae in rain forests of eastern Australia. The 5 genera at bottom of the diagram are primarily tropical and subtropical; the other genera and tribes, primarily south temperate. See text for further details.


Minor, wholly independent faunas of flightless Carabidae
Tip-of-pen. rain forest
Mid-pen. rain forest
Cooktown
Cairns
Townsville
Eungella
Tropic of C.
Q/NSW border
Dorrigo-Ebor
Mt. Royal Rge.
Sydney
NSW/V border
Water gap
Tasmania
Flightless Trechini
Eurylychnus
Promecoderus
Percosoma
Chylnus
Stichonotus etc.
Calyptogonia
Pseudagonica
Agonica
Broscini
Migadopini
Agonicini
Leiradira
Trichosternus
Mystropomus
Pamborus
Notonomus

is world-wide in distribution. It includes both flying and flightless genera, but the flying genera usually live beside standing or running water and are not forest-living geophiles. Flightless geophile Trechini are numerous both north and south of the tropics. In Tasmania they are numerous in south temperate rain forest and hardly enter other habitats at low altitudes, although some occur in open country above timber line, on cold mountain tops. Flightless Trechini are less numerous but still widely scattered in wet forests and on mountain tops in southern Victoria, including the Otway Ranges (Moore 1960), east nearly to the New South Wales border and north to Mt. Kosciusko in southern New South Wales, and endemic species perhaps representing one original flightless stock of spotted *"Trechus"* are isolated on the Mount Royal Range, the Dorrigo-Ebor plateau, and the McPherson Range on the Queensland border.[6]

The tribe Migadopini (Jeannel 1938; Darlington 1960, p. 663) is confined to the southern hemisphere, with different genera localized in Tasmania and southeastern Australia, New Zealand, and the southern tip of South America, etc. Two flightless genera of the tribe occur in Tasmanian rain forest: *Calyptogonia* is confined to Tasmania; *Stichonotus* extends to the mainland, but only to the Otway Ranges. A third Australian genus of the tribe is known from a single specimen collected long ago near Kiama south of Sydney, and a fourth genus occurs still farther north, in subtropical forest on the low (*c.* 2,000 ft.) Comboyne plateau at about 31° 35′ S. This last genus, *Decogmus*, differs from all other Migadopini in being winged.

Finally, the flightless tribe Agonicini is confined to Tasmania and southeastern Australia (Moore 1960). There are two genera. One is widely distributed in Tasmania and occurs also in the mountains of southern Victoria east of Melbourne (B. P. Moore, in letter). The other is confined to the mainland, including the Otway Ranges and the "Victorian Alps," north to Mt. Kosciusko. Agonicines live on the ground in rain forest, and sometimes in open snow gum woods on mountains.

Although there are other Carabidae in Tasmanian rain forests (especially various Pterostichini and Licinini) the four tribes just discussed make up a large part, and zoogeographically the most important part, of the flightless wet forest Tasmanian carabid fauna. It will be seen from details given above that all four tribes occur both in

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[6]A second *"Trechus", diemensis* Bates, extends from Tasmania and southeastern Australia north to the McPherson Range, but this species is winged or dimorphic.

Tasmania and on the adjacent mainland of Australia, but that they all diminish rapidly northward.

The transition of selected elements of the flightless geophile carabid faunas of tropical and south temperate rain forests is diagrammed in Fig. 7.

Isolated Australian Faunules

To return to the five carabid genera discussed above as characteristic of the main tropical and subtropical rain forests, these genera have distributions that are alike in many details. Within the main (base-of-peninsular) tropical rain forest system, they all have almost the same northern limits and (excepting perhaps *Leiradira*) the same southern limits. All are represented on the Eungella Range. In South Queensland, all apparently find their northern limit on Mt. Jacob (except that *Trichosternus cordatus* extends farther north in drier woodland), and all extend well into New South Wales, although they reach different limits there. They illustrate a general fact, that the carabid faunas of the main tropical and subtropical rain forest systems of eastern Australia, although separated by several hundred miles of comparatively dry country, are fundamentally similar, dominated by the same tribes, and share many genera some of which coincide remarkably in details of distribution, although some other genera and most species are different. However three isolated pieces of Australian rain forest have carabid faunules that do not fit into this main pattern. They are the tip-of-peninsular and mid-peninsular rain forests of Cape York and the rain forest on the Elliot Range south of Townsville.

The tip-of-peninsular tract is light rain forest and is limited both botanically and zoologically. For example, stinging trees *(Laportea)*, which occur in other Australian rain forests and in New Guinea, are apparently absent in the tip-of-peninsular forest, and land leeches and itch mites, which are pests in rain forest elsewhere, are apparently absent in the tip-of-peninsular tract. The winged Carabidae of this tract are not remarkable, except that they include New Guinean species. But the flightless Carabidae form a faunule wholly different from that of any other rain forest, consisting (so far as I could find) of only two flightless species. One is *Mecynognathus dameli* Macl., an enormous carabid, the largest males 2½ inches long with mandibles like stag beetles. The genus occurs nowhere else on earth, although it may be rather closely related to *Paranurus* (see below). The other is a large flightless *Clivina* (probably *kershawi* Sl.), which is fairly common both in the rain forest and in adjacent savannah woodland. The nature of this forest and of its flightless Carabidae suggests that

the tip-of-peninsular tract is not a remnant of a larger, continuous rain forest but has been constituted or reconstituted separately, by gradual accumulation of a limited variety of plants and animals.

The mid-peninsular rain forests of Cape York are heavier and more extensive than the tip-of-peninsular tract, more like the base-of-peninsular forests at least superficially, but their flightless Carabidae form a second independent faunule. None of the flightless genera characteristic of the other rain forests is represented in the mid-peninsular system. In their place is a single large species of *Paranurus*. This is a genus of probably only one, geographically variable species, which occurs from the tip of Cape York (and islands off the tip) south to below Cairns mainly in good savannah woodland. In most parts of its range it apparently does not enter rain forest, but it has done so in the mid-peninsular system, where it is now widely distributed. It seems to have invaded this system recently. An earlier invasion of the tip-of-peninsular rain forest by the ancestral stock of *Paranurus* may have produced *Mecynognathus*. There is also in the mid-peninsular rain forest a flightless *Coptocarpus,* but it is small and rare and I am not sure of its habitat or relationships. And also in this forest is a large form of *Lesticus chloronotus* Chd. It is winged, but its distribution and behavior suggest that it may eventually become flightless, as several stocks of the same genus have done in New Guinea. The Carabidae, then, suggest that the mid-peninsular rain forest has not been connected with the main base-of-peninsular system but, like the tip-of-peninsular tract, has derived or is deriving its flightless Carabidae independently.

The rain forest on the Elliot Range is poorly known. The only insect collecting ever done in it, so far as I know, was done March 2, 1958, when my son and I climbed from Double Creek to near the peak of Sharp Elliot and worked for three or four hours in the forest there. It seemed to be real but rather light rain forest. We found there series of two conspicuous flightless Carabidae: a very big *Nurus* and a *Notonomus*, both endemic. No trace of the four other genera (other than *Notonomus*) discussed above as characteristic of the main tropical and subtropical rain forests of Australia was found. Judging from my experience elsewhere, we would probably have found specimens or fragments of other species if the carabid fauna were diverse. I think, therefore, that the rain forest of the Elliot Range probably has a limited, endemic faunule of flightless Carabidae presumably received across a barrier and not by way of continuous rain forest. The valley that separates the Elliot Range from the main mountain

system of North Queensland is not much more than ten miles wide, but it seems to have been a more effective barrier than the much wider gaps of dry hilly country between the North Queensland, Eungella, and South Queensland rain forest areas.

Summary of Transition from New Guinea to Tasmania

The transition of wet forest carabid faunas from New Guinea to Tasmania involves two main changes. First, between the rain forests of New Guinea and those of tropical Australia is a complete change of flightless stocks of Carabidae and also a change from Agonini to Pterostichini as dominant tribes, although the change is overlain and superficially concealed by many winged species and genera of Carabidae that are common to New Guinea and Australia and that form a broad and complex transition, not fully described here. Between the tropical rain forests of North Queensland and the subtropical ones of South Queensland etc. are very many changes of species and genera but no fundamental change in the nature of faunas or in dominant groups. The second main change is farther south, and is a complex transition from tropical to south temperate groups. The area of transition (of overlapping and mixing of faunal elements) is from the southern edge of Queensland to Tasmania. And the transition involves not only changes of species and genera but a second partial change of dominant tribes, from Pterostichini as principal dominants to (in Tasmania) dominance shared by Broscini and Trechini (and Licinini) as well as some Pterostichini. This change has been described as it occurs among selected flightless geophile Carabidae, but it is reinforced and made more complex by changes of winged Carabidae too.

The whole transition of wet forest carabid faunas from New Guinea to Tasmania might be described as a very irregular stepcline of flightless groups overlain by a more regular transition (or cline of many smaller steps) of winged groups. The flightless Carabidae of the isolated rain forests of Cape York and the Elliot Range are outside the main pattern and complicate it, and of course the situation as a whole is much more complex in detail than I can describe here.

Historical Implications: Two Land Bridges

It is a good working principle of zoogeography that situations should be analyzed first by study of the best known and most significant groups of animals, especially mammals, but that other groups may add important details to what the mammals show. In the present case, two former land bridges are involved: from New Guinea to Australia

and from Australia to Tasmania. Mammals show, by occurrence of many identical or closely related species on opposite sides of the existing water gaps, that both bridges did exist recently and that some forest-living animals crossed both of them. Carabidae show additional, different things about the two bridges. In the case of the Australian-Tasmanian bridge, the Carabidae agree with the mammals. Many wet forest Carabidae including many flightless ones evidently crossed this bridge without meeting important ecological barriers, although cold climate stopped some other animals, especially some reptiles (Darlington 1960, p. 659). In the case of the New Guinea-Australian bridge, however, the flightless rain forest Carabidae show that there was an ecological barrier upon the land, and that the barrier existed for a long time. New Guinea and Australia cannot have been connected by a continuously rain-forested ridge within the time of existing carabid faunas. The recent connection was evidently low and rain forest was probably not continuous across it, although it was nearly enough continuous to allow certain forest trees, mammals, birds, and winged insects to get across. These organisms probably crossed the bridge by way of more or less separate forest "stepping-stones" and strips of gallery forest that did not allow continuous passage of flightless rain forest Carabidae, which do not disperse easily across even narrow gaps of unsuitable land. Rain forest is discontinuous on Cape York now. The Carabidae suggest that it has been so for a long time in the past, and that conditions on Cape York now are like the conditions that existed on the land bridge when New Guinea and Australia were connected.

Historical Implications: Climatic Fluctuations

The present distribution of wet forest Carabidae shows that many of them have been able to move up or down the eastern edge of Australia between North and South Queensland, across what are now wide gaps of comparatively dry country. The degree of relationships of different Carabidae in the tropical and subtropical rain forest systems varies. In some cases (*e. g. Pamborus* of the *tropicus* group) the North and South Queensland representatives of single original stocks are only slightly differentiated, but in other cases (*e. g. Leiradira* and its allies) they have diverged as subgenera or genera. This suggests either several periods of dispersal and isolation, accompanying fluctuations of rainfall and rain forest, or occasional trickling of dominant wet forest Carabidae across the drier gaps of central Queensland. In either case wet forest Carabidae seem to have followed a rather narrow path along the continental divide, and have usually

not been able to reach such slightly isolated places as the rain forest on the Elliot Range. The whole pattern, of occasional or limited exchange between North and South Queensland and of isolation of endemic faunules on the Elliot Range and in the Cape York rain forests, is consistent with climates and forests fluctuating only within moderate limits, not profoundly.

Ecological Correlations

It is a fact not sufficiently understood by some zoogeographers that the climatic zones, the differences between tropical and cool temperate climates, are very important to Carabidae and other insects. In eastern Australia, where climate is the only permanent barrier to dispersal, many old groups of Carabidae are confined to either the tropical (including subtropical) or the cooler south temperate areas. Evidently whole tribes may persist for long periods in small areas protected only by climatic barriers, and even dominant tribes do not always easily cross from one climatic zone to another.

Carabid distribution is correlated with climate and ecology in several more specific ways. For example some rain forest Carabidae, including five genera specially considered above, seem to be more strictly limited to rain forest in the tropics than in the south temperate zone. This suggests that ecological factors are more intense in the tropics, as they may well be if temperature and evaporation rates are involved. That ecological factors are intense in the tropics is suggested also by groups of Carabidae that occur in diverse habitats in the temperate zones but enter or cross the tropics only when associated with surface water, which probably tempers the intensity of tropical climate. I have discussed this elsewhere (1959, especially pp. 332, 342). In Australia, for example, the only Trechini that occur in the tropics are winged hydrophiles: *Perileptus* and *Trechodes* by running water and *Trechobembix* (which extends north to Cairns) in deep swamps. *Mecyclothorax* occurs in many habitats in temperate southern Australia, but I found only one species (apparently *cordicollis* Sl.) in the tropics, in thick vegetation over deep, cool water on the Atherton Tableland. And *Notagonum ("Agonum") submetallicum* (White), which, though always associated with water, occurs in a variety of waterside habitats in both humid and arid parts of south temperate Australia, I found in the tropics (Atherton Tableland) only in thick vegetation over cool, moving water.

There is also a notable correlation of wings and flight of Carabidae with climate and altitude. Carabidae (mostly geophiles) often become flightless at low altitudes in temperate climates, and on moun-

tains everywhere, but rarely at low altitudes in the tropics. The fewness of flightless Carabidae at low altitudes in New Guinea is an example. I have discussed this subject, with other examples, elsewhere (1943).

Finally there is a partial correlation between size of Carabidae and climate. Very large Carabidae (over 1 to 2½ inches long) are numerous in the forests of warm temperate to tropical eastern Australia but relatively few or absent in both cool temperate Tasmania and wholly tropical New Guinea. If *Catadromus tenebrioides* (ol.) is introduced, as I think it is, the largest carabids in New Guinea are hardly an inch long and few are that large. I suspect that this correlation has a complex ecological basis which may include direct action of physiological factors, correlation of size with state of wings and flight, and competition with other insects. Of insects that might compete with carabids, ants are most obvious. I have suggested (1943, p. 42, Fig. 4) that ants may take the place of most flightless geophile Carabidae especially in the lowland tropics.

Geographical History of Carabidae

Carabidae, like other old, complex groups of animals (mammals etc.), have presumably had complex geographical histories, with successive dominant groups evolving, spreading over the world, and replacing older groups. The present distribution of Carabidae in the Australian Region may reflect this. Some localized tribes that are now confined to the cool south temperate zone may be remnants of an ancient fauna (see Darlington 1960 for further discussion of some of these groups). Pterostichini, now dominant in most of Australia, may be more recent and may be replacing more ancient Carabidae. And Agonini may be still more recent, now dominant in New Guinea (and in the whole tropical Asiatic-Australian area), and spreading to Australia.

Pterostichini and Agonini tend, as dominant tribes, to be complementary over the world as a whole. I have discussed this before (1956, pp. 1-3), but what I said then is worth repeating briefly now, with counts of species brought up to date. Both tribes are cosmopolitan, but unevenly so. In some parts of the world they occur in nearly equal numbers, in others, one tribe or the other is overwhelmingly dominant. The tribes tend to be complementary within the Australian Region, as already indicated. In Australia itself (with Tasmania) Pterostichini are dominant, with more than 350 known species against probably less than 20 species of Agonini, a ratio of nearly 40/1. But

in New Guinea Agonini are dominant, with considerably more than 100 known full species (some discovered since my 1952 paper) against about 40 species of Pterostichini (manuscript in press), a *reversed* ratio of about 3/1.

One reason for the number of Agonini in New Guinea is that species of this tribe have multiplied on the mountains there. In Australia, however, Pterostichini, not Agonini, have multiplied in what seem to be comparable habitats on the mountains. This difference can hardly be accounted for in simple ecological terms but is probably due to a complex combination of ecological, historical, and geographical factors. Over the world as a whole, there is a tendency for Agonini to be better represented in the tropics; Pterostichini, in the temperate zones. Also it is probable that Agonini, which are phylogenetically less diverse, are more recent in origin than Pterostichini and that they have dispersed more recently. It is therefore likely that Pterostichini are dominant in Australia partly because Australia is more temperate than tropical in climate and partly because Pterostichini reached Australia before Agonini did, and it is likely that Agonini are dominant in New Guinea partly because the climate there is fully tropical and partly because the carabid fauna of New Guinea is more recent in its origins than that of Australia, as I think it is. Add to this that the mountain carabid faunas of Australia and New Guinea have been derived independently, each from the lowland fauna adjacent to it, and not by dispersal along a connecting mountain chain, and we have an adequate and probably correct explanation of the great difference in composition of the carabid faunas on the mountains of Australia and New Guinea.

As to direction of recent movements of Carabidae, movements of (winged) species have evidently occurred in both directions between Australia and New Guinea, although I cannot take space to give details now. Movements have apparently occurred also in both directions between the tropical and subtropical forests of Australia. This is indicated by the relationship of the species now on the Eungella Range (p. 13), although I am not ready to give further details now. South of the tropics, patterns of distribution (Fig. 7) suggest withdrawal of cool temperate groups and southward spreading of tropical or subtropical groups. This is probably primarily an adjustment to recent warming of climate rather than an invasion of south temperate habitats by tropical Carabidae, although *Pamborus, Trichosternus,* and *Notonomus* have invaded *Nothofagus* forest on high plateaus in New South Wales.

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